The laminar origin of sensitivity to higher-order image statistics in macaque visual cortex

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Overview

Extraction of local features (e.g., edges and lines) and surface properties are the important first steps in extracting meaning from natural images. Analysis of higher-order statistics (HOS's) is critical for these processes, but it is as yet unclear where and how the underlying neural computations occur. To approach this question, we studied neuronal responses to a library of artificial visual textures in which individual kinds of third- and fourth-order statistics are introduced. The stimulus library included higher-order statistics that are perceptually salient, as well as those that are not (Victor and Conte 1991).

We find that many neurons in V1 and V2 are selectively sensitive to higher-order statistics, and, across the population, the pattern of sensitivity mirrors psychophysical findings. The prevalence of sensitivity to higher-order statistics is modest in V1 and increases markedly in V2. A laminar analysis of response dynamics suggests that intra-cortical processing and feedback involving the supragranular layer plays a critical role.

Methods

Preparation: Single-unit recordings using multitetrode arrays were made in V1 and V2 of macaques, anesthetized with propofol and sufentanil and paralyzed with vecuronium or rocuronium.

Visual stimuli: The stimulus library consisted of random checkerboards and six types of textures with higher-order correlations (1024 examples of each type). Figure 2 shows one example of each of these stimulus types (upper panel: for each type, the icon indicates the spatial organization of its correlations). The "even" and "odd" textures have visually salient fourth-order correlations. The "white triangle" and "black triangle" textures have visually salient third-order correlations. The "wye" and "foot" textures have fourth-order correlations, but these correlations are more difficult to perceive (Victor and Conte, 1991). For each type of texture, all 1024 examples (two repetitions each) were presented during the experiment, each for 320 ms, in interleaved fashion. Check size was scaled to the receptive field size of a target neuron at one tetrode, and orientation was set according to the orientation preference of the target neuron.

Spike sorting: After bandpass filtering (300 to 9000 Hz) and thresholding, waveforms were clustered using custom versions of KlustaKwik and Klusters (Hazan et al, 2006). Features consisted of peak amplitudes and principal components.

Analysis: Local linear regression (Loader, 1999) was used to calculate smooth firing rate functions elicited by stimuli with each kind of image statistic. Significance of the difference between two firing rate functions was determined by comparing the actual difference with the distribution of differences computed from 3000 shuffles. Only shuffles between responses collected at nearby times were considered, to account for possible non-stationarity. The False Discovery Rate (FDR) method was used to correct for multiple comparisons (one at each 5 ms time bin, from 50 to 250 ms after stimulus onset).

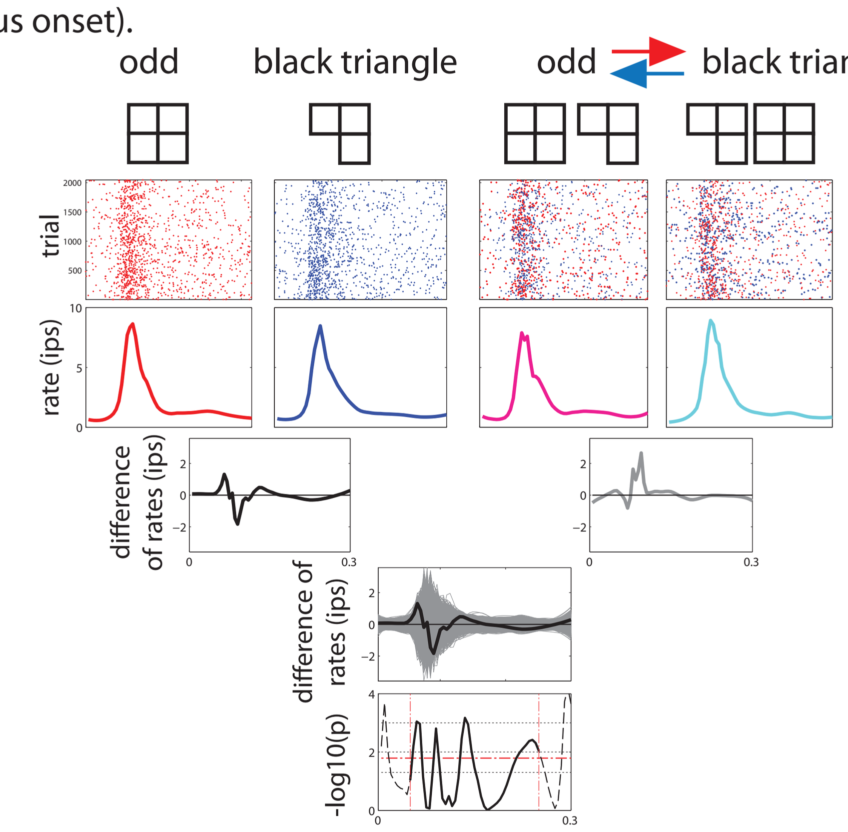

Fig. 1. Estimation of significance of differences between neuronal responses to stimuli enriched by specific HOS's. A difference is considered significant if a shuffle test yields $p<0.05$, with False Discovery Rate (FDR) correction over the interval from 50 to 250 ms following stimulus onset. On the lower panel, the red dashed lines indicate the 50-to-250 ms window and the FDR-corrected p=0.05 criterion; gray horizontal dashed lines indicate the uncorrected *p*-values.

Results: individual neurons

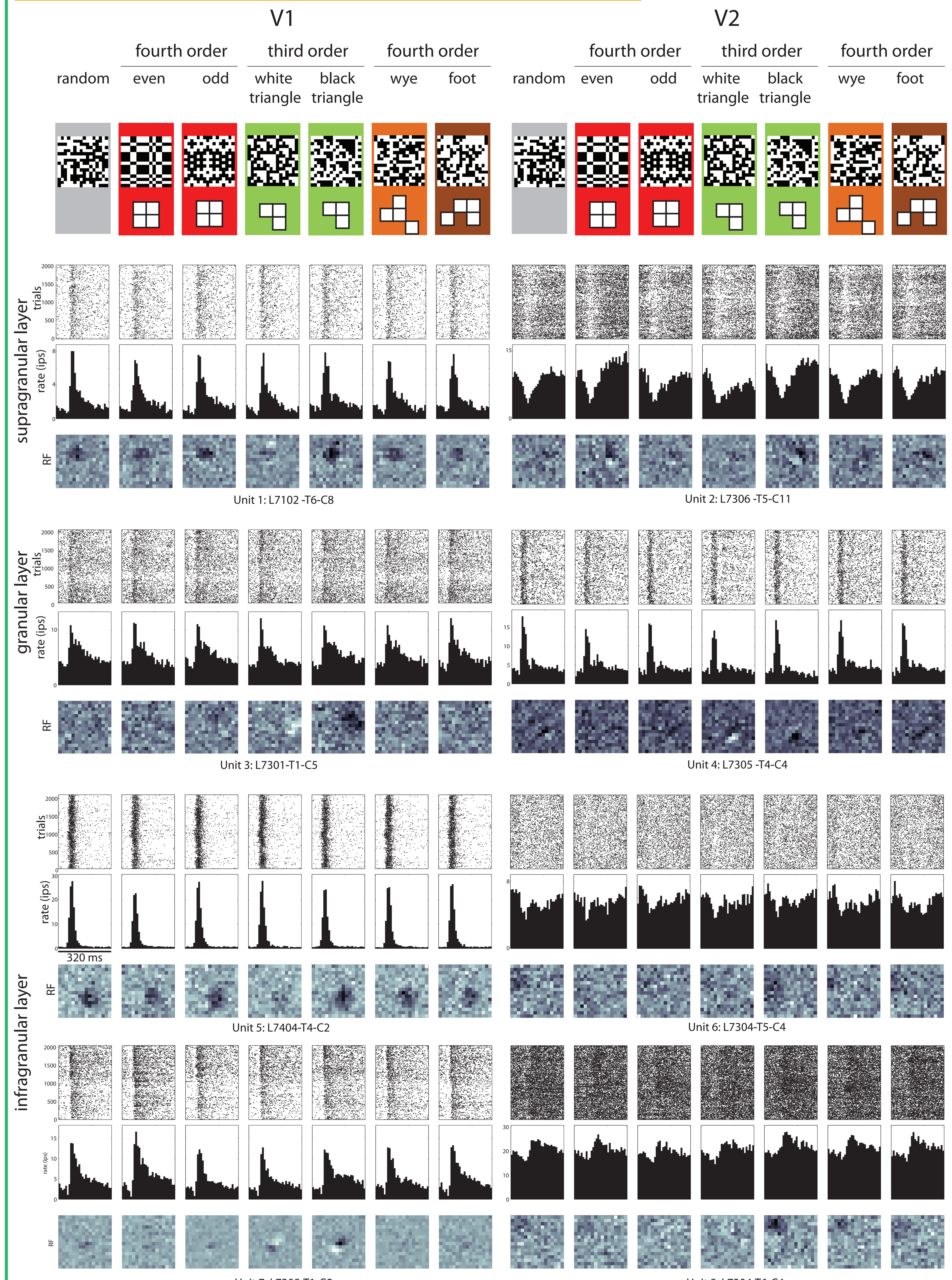

Fig. 2. Responses to stimuli enriched by specific HOS's (rasters and PSTH's), and receptive field maps obtained by reverse correlation. Within each neuron, the responses elicited by each HOS class had similar dynamics, but differential responses to individual kinds of HOS's were also evident. For some neurons, reverse-correlation maps were present for some HOS stimuli but not for others (Unit 3, 4, 6, 7, and 8), or had substructure that depended on the kind of HOS (most examples). Across the population, responses were more transient in V1 than in V2. Inhibitory responses were present in both areas, but more often in V2 (Unit 2, 6, 8, and possibly 7).

Results: population

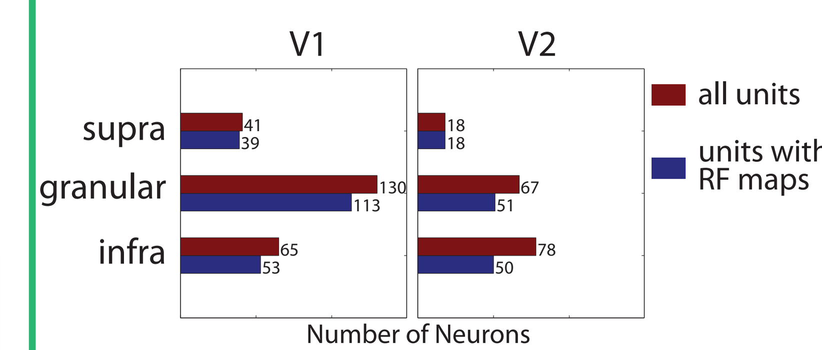

Fig. 3. Number of neurons studied, by region (V1 vs. V2) and layer (supragranular, granular, infragranular). The red bar indicates the total number of units isolated; the blue bar indicates the number of units that had an identifiable receptive field map via reverse correlation for at least one kind of HOS.

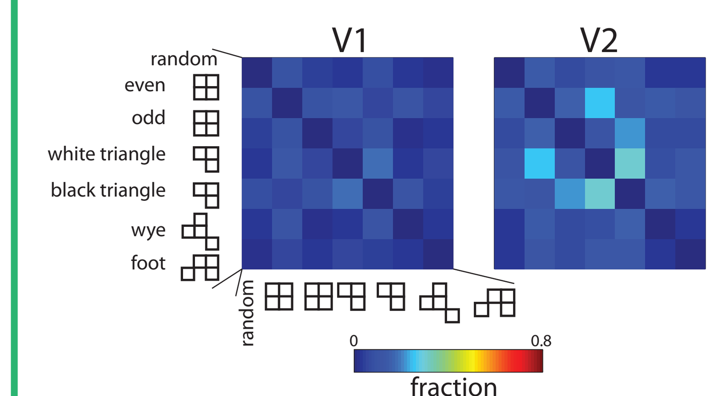

Fig. 4. Population summary for discrimination of different kinds of HOS's. Entries in each array correspond to a pair of HOS stimuli, indexed by row and column. Upper panels: the fraction of neurons that responded differentially to the corresponding pair of HOS stimuli. Differential responses are more prominent in V2 than V1.

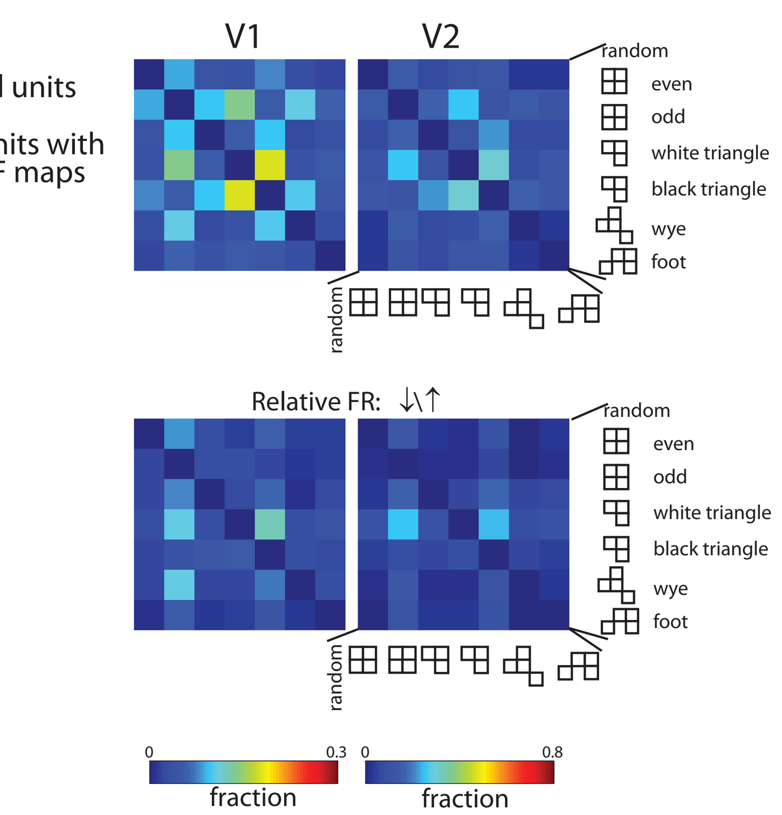

Fig. 5. Further analysis of the population pattern of responses. Upper panels: data from Fig. 4 rescaled so that the pattern of responses in V1 is evident. Differential responses occur primarily among the even, odd, and triangle textures, and between these textures and the subset consisting of random, wye, and foot; these correspond to the differences that are psychophysically salient. Lower panels: breakdown according to the sign of the response difference. Each entry indicates the fraction of neurons that had a larger response to the HOS labeling its column, than to the HOS labeling its row. This shows that differential responses are consistent across the population.

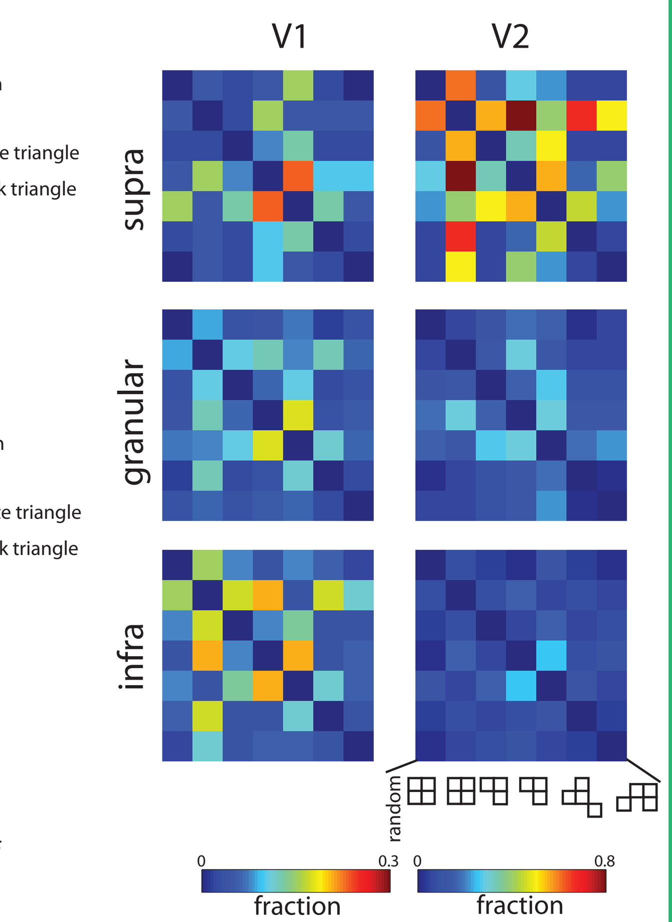

Fig. 6. Laminar analysis of discrimination of different kinds of HOS's. As in Figs. 4 and 5 (upper), array entries correspond to the fraction of neurons that responded differentially to the corresponding pair of HOS stimuli. Differential responses were more prominent in the supragranular layers than the granular layers.

Laminar analysis of response dynamics

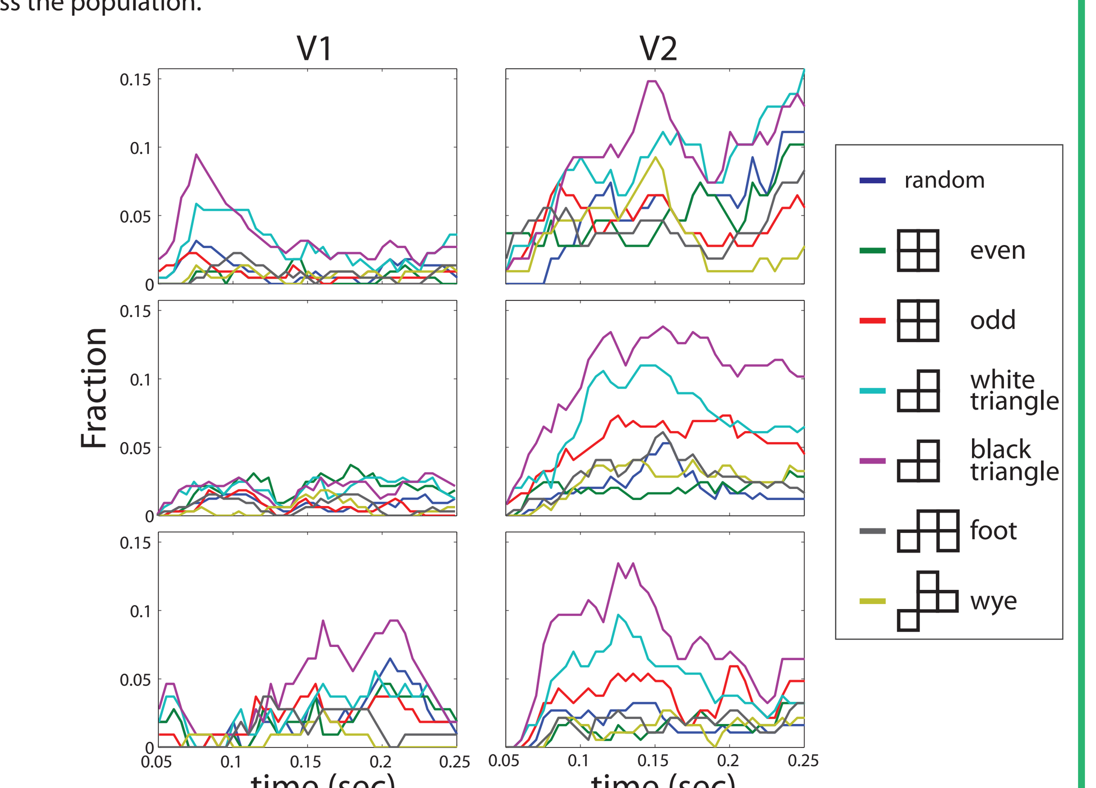

Fig. 7. Laminar analysis of responses dynamics in V1 and V2. Each curve indicates the fraction of neurons that shows a differential response between one kind of HOS and any of the others, as a function of time following stimulus onset. There is a systematic dependence of dynamics on cortical area and layer. In V1, differential signals appear earliest in the supragranular layers, and then in the granular layer (even though the response latency, as expected, is shortest in the granular layer). There is a second mode of differential responses from 150 to 250 ms in the granular and infragranular layers. In V2, differential responses appear with a similar timecourse in all layers, and are more sustained than in V1.

Conclusions

1. Responses of individual V1 and V2 neurons are selectively sensitive to higher-order statistics.
2. Across the population, the pattern of selectivity corresponds to human psychophysical findings (Victor and Conte, 1991).
3. Laminar analysis indicates that neural selectivity arises as a result of processing both in V1 and in V2.
   The dynamics of HOS sensitivity suggest that feedback among the laminae within each cortical area plays a crucial role.

References

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